PARTHENOGENESIS AND THE INHERITANCE OF COLOR PATTERNS IN THE GROUSE LOCUST *PARATETTIX TEXANUS* HANCOCK.

ROBERT K. NABOURS AND MARTHA E. FOSTER.[1]

Introduction.

Newell (1914) reported segregation of genetic factors in parthenogenesis, wherein hybrid Carniolan-Italian queen bees gave equal numbers, respectively, of pure Carniolan and Italian drones. Previously, Perez (1879) and Cuénot (1909) had noted variations among the drones from hybrid queens, but more than one pair of factors had apparently been involved. Observations were made in 1923–24, in the apiary of the Kansas Agricultural Experiment Station of the offspring of separate queen bees considered hybrid. The drones varied greatly in their characteristics, especially with respect to color, ranging from black, through various degrees to the yellow of the Italian. These queens thus exhibited a considerable degree of genetic complexity, indicating the presence of two or more independent pairs of factors for color and other characteristics.

Parthenogenesis in the grouse locusts was first recognized in 1915, in attempts to crossbreed males of *Paratettix texanus* with females of *Apotettix eurycephalus*. It was noted that the offspring from such matings were exclusively females, and carried the color pattern of the female of the pair if she were homozygous, or segregated into her component, or cross-over patterns if she were heterozygous. Then it was soon ascertained that *A. eurycephalus* females which had never been exposed to males of any kind behaved in these respects precisely as did those exposed to *P. texanus* males. As many as 4,470 females and seven males produced in parthenogenetic breeding, mostly from females which had not been exposed to males at all, many showing segregation and crossing-over of factors for color patterns, had been re-

[1] Contribution No. 110, Department of Zoölogy, Kansas Agricultural Experiment Station.

corded by August 1, 1918 (Nabours, 1919). Later, some females of *A. eurycephalus* were bred seven consecutive generations parthenogenetically, and there was further rather extensive experimental breeding of this species both bisexually and parthenogenetically (Nabours, 1925, 1929).

Segregation of factors for color patterns in parthenogenesis was found to occur also in *Telmatettix aztecus* (Nabours and Snyder, 1928). There have been a few females of *Tettigidea parvipennis pennata* produced in this laboratory from unmated parents. One unmated individual of this species of the genetic composition F/M, (for color patterns see Bellamy, 1917), gave two F/F and three M/M females (1922, unpublished).

Whiting (1921a) reported on the wasp *Hadrobracon brevicornis,* wherein the unmated females, hybrid for black and orange eyes, gave nearly equal numbers, respectively, of black and orange eyed males. He also reported a factor for lethal (Whiting, 1921b) which exhibited 19.5 per cent. of crossing over with the factors for orange and black eyes in parthenogenetic breeding.

Hybrid moths from the crossing of *Tephrosia bistortata* males with *T. crepuscularia* females reproduced parthenogenetically, and there was segregation with respect to wing color and pattern. The unmated females of neither species alone would give progeny. In connection with the report of these results, the authors (Peacock and Harrison, 1925) advanced the *hypothesis that parthenogenesis was consequent upon hybridity.* In a later paper (1926), these investigators adduced from my tables (Nabours, 1919, 1925) that all the parthenogenous females of the grouse locust *A. eurycephalus* had been hybrids from the crossing of one variety of the species from Tampico, Mexico, with another from the region of Houston, Texas. They welcomed this as evidence constituting strong confirmation of their hypothesis.

Progeny have resulted in this laboratory in three of eight attempts to cross males of *A. eurycephalus* with females of *P. texanus,* once in 1912 and twice in 1915. In the first case, the female, one generation from Many, Louisiana, gave five females, all appearing to be like herself. In the other cases, an I/P female gave one I/I, or +/I, and two P/P, or +/P, females, and a B/C female gave two C/C, or +/C, females. Both these parents

were one generation from Houston, Texas. Since these three females had been probably also exposed to brothers, and as none of the progeny was tested, the results had been regarded with doubt. However, a reëxamination of the records, in the light of further experience, strengthens the possibility that these were also cases of parthenogenesis.

Females which are exposed to males of any kind are considered as having reproduced parthenogenetically (1) if the contrasting dominant characteristics of the males do not develop in the offspring, (2) if practically all the offspring are females, or (3) if the offspring, when bred further, are found to be homozygous for those factors for which they should be heterozygous had the eggs been fertilized. At least two, or sometimes all of these criteria are applied in the determination of each case. It is obvious that, in those matings where the males give some or all recessive gametes, a proportionate number of the female progeny which are not tested by further breeding, or determined histologically, may possibly be, in fact, of parthenogenetic origin.

Parthenogenesis in *Paratettix texanus*.

Parthenogenesis in *Paratettix texanus* was first definitely recognized on November 14, 1922, when the offspring of a pair of heterozygous individuals of contrasting dominant color patterns exhibited segregate patterns of the female only, and all were females (Table II., item 1). During the five years following, until November, 1927, 32 other females that had been similarly exposed to males of contrasting dominant color patterns produced 187 recorded females and one male, all bearing exclusively the maternal characteristics, Table II., items 2–17, 30, 32–34, 36, 40, 44–50, 52, 79 and 81. Of these offspring, 26 were successfully tested in matings, or by reproducing again parthenogenetically, and all were found to have been homozygous for the dominant maternal patterns, Table II., and V.

Some of the males to which the 33 females had been exposed were thought to have been impotent, while the others died, or escaped from the cages before matings occurred. In both *Apotettix eurycephalus* (Nabours, 1919, 1925, 1929) and this species, *P. texanus,* it has appeared that any female, if potent at all, re-

produced bisexually, rarely, if ever parthenogenetically, when mated with a potent male.

These 33 cases of parthenogenesis among females exposed to males have occurred during the last quarter of a period of the breeding of *P. texanus* covering nineteen years, although there had been many opportunities for parthenogenesis from the beginning. In numerous cases males had died, or escaped from the cages after the matings had been made, and the females remained for long periods without offspring ensuing. The matings and records of the entire period have been made in such a manner that, with comparatively few exceptions, parthenogenesis would have been indicated.

Following the observations of the first few cases of occasional parthenogenesis among females that had been exposed to males, and having in mind the experiences with *A. eurycephalus* (Nabours, 1919, 1925, 1929) a number of females of *P. texanus* were separated from the males. From 75 of these which were not exposed to males after becoming adult, 625 offspring were secured and transferred from the parent to the progeny cages. Of these, 393 females and one male became large enough to permit records being made of their sex and color patterns, and there were seven the sex of which was not noted (Table II.).

Materials and Methods of Breeding.

The specimens used in these experiments were taken from the stocks of *P. texanus* which had been bred in the greenhouse, beginning with individuals secured at Houston, Texas, in September, 1908 (Table IV.). New specimens had been added nearly every year, during the first 13 years, or until 1921, from Houston, San Antonio, Sugarland, Mackay and Beaumont, Texas, and Many and Baton Rouge, Louisiana, but principally from Houston and Sugarland. Specimens were secured and added to the stocks during the last five years from San Antonio, Houston, Sugarland, and, in addition, from Austin and College Station, Texas. Therefore, there has been abundant opportunity for hybridization of probably slightly differing varieties, a feature which will be discussed farther on.

Most of the elementary color patterns of *P. texanus,* and some

of their hybrid complexes, have been previously approximately described and illustrated (Nabours, 1914, 1917, 1923, and Plate III., 1929). The full list of those employed in experimentation up to date may be described, though inadequately, as follows: (1) +/+ (old AA), mottled gray, a pattern common to practically all the grouse locusts, and now considered the normal recessive, or "wild type"; (2) B/B, white over pronotum and parts of posterior femora; (3) C/C, white anterior pronotum, posterior dark or mottled, reddish brown legs; (4) Cext/Cext, the same as C/C, but with an extension of the white of the anterior pronotum posteriorly, and the line between the white anterior and dark posterior is not sharp; (5) Cof/Cof (old QQ) practically the same as C/C, but with red middle legs and conspicuously orange colored femora of the jumping legs; (6) D/D, the same as +/+, but with conspicuous white spots on hind femora; (7) E/E, broad yellow stripes along median pronotum and on distal ends of posterior femora; (8) F/F, broad mahogany stripes along median pronotum and posterior femora; (9) S/S, broad yellowish gray, nearly white stripes along median pronotum and on distal ends of hind femora; (10) Sm/Sm (old ISIS), broad brown, slightly red stripes along median pronotum and on distal ends of posterior femora (distinctly different from the other stripes and the only mutant observed to occur in the greenhouse); (11) S_1/S_1, broad nearly clear white stripes along median pronotum and on distal ends of hind femora, and with red middle legs; (12) P/P, broad brown stripes along median pronotum and on distal ends of posterior femora; (13) L/L, trilineate, three nearly white lines along the pronotum and one along femora of hind legs; (14) K/K, narrow white stripe along median pronotum, and red middle legs, almost indistinguishable from K/K, of *Apotettix eurycephalus,* (Nabours, 1925); (15) J/J, conspicuous large white spot over broad part of pronotum, identical with Y/Y in *A. eurycephalus* (loc. cit.); (16) Jof/Jof, the same as J/J, but with prominently orange colored posterior femora and red middle legs; (17) H/H, large yellow, or orange spot covering the same area as the white spot of J/J; (18) Hm/Hm, a gray, slightly orange spot, covering the same area as the spot H/H; (19) I/I, a dark mahogany spot over the same area as that of J/J; (20) M/M,

brown all over pronotum. Hybrid M/S looks precisely like Sm/Sm. It is now thought, contrary to the previous idea, that the origin of Sm was due to the mutation of a gene closely linked with the S gene (Nabours, 1917, pp. 48, 52, 53); (21) N/N, a brown gray all over; (22) N_1/N_1, dull orange, or henna all over; (23) N_2/N_2, brilliant orange all over. These first named twenty-two factors for color patterns are extremely closely linked. Hm is the only one to have crossed over at all. Some of them may be actually multiple allelomorphs. (24) θ/θ, dense black over anterior pronotum, fading somewhat towards the posterior, and extending over the hind femora; (25) sf/sf, white spots on posterior femora, resembling D/D, but recessive in heterozygotes, and not showing well, even in homozygous condition, with some of the dominant patterns, as C, Cof, Jof; (26) ϕ/ϕ, reddish, or pink all over, hardly discernable, almost recessive in heterozygotes. These two, sf/sf and ϕ/ϕ, are the only colors so far discovered in all the grouse locusts, except the normal recessive, +/+, that can in any sense be considered recessive, and they are only partially so. These last described three are extremely loosely linked with each other and all the others, or they may be on separate pairs of chromosomes (For θ, see Haldane, 1920).

The breeding methods have been about the same as those employed in all the experiments with the grouse locusts (loc. cit.). A longer time is required to obtain offspring from unmated females, and they are fewer in numbers, than from mated ones. A comparison of the productivity of unmated individuals with their mated sisters is shown in Table I, covering the period, January–October, 1925. This comparison shows that 46.6 per cent. of the unmated females were productive, while 62.5 per cent. of their mated sisters gave offspring. The average number of offspring for the unmated individuals was 9, while the average number hatched from the mated sisters was 60.13, or more than six times as many. Sixty-seven and five tenths per cent. of the offspring hatched from unfertilized eggs, against 53.75 per cent., of those hatched from the mated sisters, were recorded. The discrepancy in the proportions recorded, however, might not have been due so much to the greater viability of the parthenogenous progenies as to the care they were given, and early age at which

records were made. These were noted every day, while the progenies of the mated sisters were part of the larger breeding projects and were recorded only in their turn, which was sometimes long after they were large enough, and after considerable mortality.

Miss Isabel Potter has had a considerable share in conducting these experiments, and the principal task in the preparation of the tables.

TABLE I.

PRODUCTIVITY OF UNMATED FEMALES COMPARED WITH MATED SISTERS (JANUARY-OCTOBER, 1925).

Months Females Were Placed in Mating Jars.	Unmated Females.				Mated Females.			
	Number of Unmated Females.	Number Productive.	Number of Offspring Transferred.	Number of Offspring Recorded.	Number of Mated Sisters.	Number Productive.	Number of Offspring Transferred.	Number of Offspring Recorded.
January.....	1	1	24	17	2	1	128	66
February....	1	0	0	0	2	2	175	100
March.....	27	23	250	188	15	14	1,078	731
April.....	7	7	32	24	0	0	0	0
May.....	12	8	75	39	5	3	402	171
June.....	31	4	26	9	33	18	665	285
July.....	18	3	20	7	9	5	168	84
August.....	0	0	0	0	0	0	0	0
September...	8	3	14	14	5	2	90	17
October.....	0	0	0	0	1	0	0	0
Totals....	105	49	441	298	72	45	2,706	1,454
	46.6% productive; average 9. offspring; 67.5% recorded.				62.5% productive; average 60.13 offspring; 53.75% recorded.			

THE EXPERIMENTS.

The data are presented mainly in tables with explanations, and their use illustrated by a few succinctly elaborated examples. The tables have cross references so that the progenitors, or posterity, both males and females, of any individual, so far as they appear to be related to parthenogenesis, may be traced. Table II. shows the parthenogenetic breeding of 108 females, composing 83 items of individuals and groups. Thirty-three of the females, items 1–17, 30, 32–34, 36, 40, 44–50, 52, 79 and 81, had been exposed to males; the other 75 had not, after becoming

adult. Table III. shows the 15 matings in which, in addition to the bisexual progeny, each female also gave from one to seven parthenogenetic offspring. Table IV. gives the sources of the male and female progenitors of the parthenogenetic individuals over a period of years in various places in nature. Table V. indicates the further breeding of the partheno-produced [1] individuals of Table II. in matings with males. This table also includes two matings, 208 and 216, in which there were also partheno-produced offspring.

Explanation of Table II.—The second column gives the sources of the females, respectively. Those of the first 31 items had no parthenogenesis in their recorded ancestry, and are referred to Table IV. where their lines may be traced to the various places in Louisiana and Texas, where their progenitors were collected. The females of the remaining 52 items, 32–83, were the daughters, or the descendants through only one, or a few parthenogenetic, or bisexual generations of these first parthenogenetic individuals of items 1–31.

The symbols, in parentheses, in the third column indicate the factors for color patterns of the males to which the 33 females were exposed. This column is blank in those items where the females were not so exposed.

The fourth column, after the X's, shows the symbols representing the factors for the color patterns of the females. The figures, in parentheses, before these, when there was more than one, show that two or three sisters of the same genetic composition were used.

The next groups of symbols and figures represent the factors for the color patterns and the numbers of the progeny. The number of males is at the left, and the number of females at the right of the hyphen, invariably; a number after a second hyphen indicates those the sex of which was not determined, items 31, 37, 51 and 67, Table II. The last numbers, in parentheses, indicate the items, or matings in Tables II. and V. where the results of the further breeding of the progeny are shown.

Elaboration of the Use of Table II.—Item 1: Table IV. is

[1] This composite word was suggested by W. R. B. Robertson.

where the ancestry of this female, which had no recorded parthenogenesis in her line, may be traced to individuals secured, over a period of several years, at several places in Texas and Louisiana. J/Sm represents the factors for the dominant color patterns of the male to which the female, B/Cof, next after the X, was exposed. The next two groups show the progeny, two females each of the segregate patterns, B/B and Cof/Cof, respectively, and exclusively of the female of the pair.

Item 42: Bis. 204–6 indicates that these females, KΘ/S, had descended through one bisexual generation, mating 204, Table V., from the parthenogenetic female, I/S, item 6, Table II. The four groups of symbols and figures show the non-crossover and crossover progeny, all females. The final figures 234–237, in parentheses, are the numbers of the matings, Table V., which give the results of the mating with males of four of these parthenogenetic progeny.

Item 55: The female parent, B/H, had descended through one, (1), bisexual generation, not noted in these data, from mating 205, Table V., the female of which, in turn, had been one of the parthenogenetic progeny of item 7, Table II. Two of these progeny, H/H, later produced 13 females, all like themselves, item 60. Dir. 55, item 60, means that the two females came directly from the parthenogenetic progeny of item 55.

Item 75: The female parent, LΘ/M, was descended from three parthenogenetic progenitresses as follows: (*a*) A Cof/Cof female of the parthenogenetic progeny of item 4, Table II., was mated, 202, Table V. An individual from this mating was, in turn, mated, and so on for four generations, five in all, when, from this fifth bisexual generation, the LΘ/M female was taken. Bis. (4) 202–4 = four bisexual generations to mating 202, five bisexual generations in all, to parthenogenetic item 4. (*b*) Another parthenogenetic progenitress was from item 37, bred bisexually in mating 208, and then another bisexual generation, not noted in these data, to item 75. (c) The line of descent then extends from item 37, through one biparental generation, 203, to the parthenogenetic female, item 6, Table II. It is to be observed that this female, item 75, had none of the color characteristics of her three respective parthenogenetic progenitresses, items 4, 37

TABLE II.

SHOWING PARTHENOGENESIS IN *Paratettix texanus*.

Items.	Source.	Males.	Females.	Offspring.
1	Table IV	(J/Sm)	× B/Cof	B/B 0–2, Cof/Cof 0–2
2	Table IV	(Cof/KΘ)	× B/P	B/B 0–2, P/P 0–1
3	Table IV	(KΘ/P)	× B/Cof	B/B 0–1, Cof/Cof 0–1 (200)
4	Table IV	(B/KΘ)	× Cof/S	Cof/Cof 0–5, S/S 0–3 (201, 202)
5	Table IV	(B/I)	× J/N_2	J/J 0–3, N_2/N_2 0–3
6	Table IV	(Jof/K)	× I/S	I/I 0–2, S/S 0–1 (203, 204)
7	Table IV	(CofΘ/K)	× E/H	E/E 0–7, H/H 0–5 (205)
8	Table IV	(JΘ/K)	× J/P	J/J 0–2, P/P 0–1 (206)
9	Table IV	(C/EΘ)	× B/Jof	B/B 1–5, Jof/Jof 0–8
10	Table IV	(+/KΘ)	× C/N_1	C/C 0–2, N_1/N_1 0–3 (207)
11	Table IV	(+/BΘ)	× C/Jof	C/C 0–1, Jof/Jof 0–1
12	Table IV	(L/Sm)	× Hm/MΘ	Hm/Hm 0–3, HmΘ/HmΘ 0–4, M/M 0–3, MΘ/MΘ 0–5 (209, 210, 211, 212, 33, 34, 247)
13	Table IV	(K/S)	× +/J	J/J 0–1 (213)
14	Table IV	(CofΘ/E)	× Hm/Hm	Hm/Hm 0–2
15	Table IV	(N/S)	× BΘ/Hm	B/B 0–1, BΘ/BΘ 0–1, Hm/Hm 0–2, HmΘ/HmΘ 0–1
16	Table IV	(EΘ/K)	× +/B	+/+ 0–2, B/B 0–4
17	Table IV	(E/L)	× F/HΘ	F/F 0–1, H/H 0–2, HΘ/HΘ 0–6 (249)
18	Table IV		Cof/S	Cof/Cof 0–3, S/S 0–2
19	Table IV		(3) K/K	K/K 0–13
20	Table IV		(2) K/M	K/K 0–3, M/M 0–3 (233, 76)
21	Table IV		(2) C/K(Φ)	C/C 0–2, K/K 0–2, CΦ/CΦ 0–1, KΦ/KΦ 0–1 (227)
22	Table IV		(2) Jsf/Jsf	Jsf/Jsf 0–5 (35)
23	Table IV		KΘ/P	KΘ/KΘ 0–1, P/P 0–2
24	Table IV		HΘ/S_1	HΘ/HΘ 0–2
25	Table IV		(2) BΘ/H	H/H 0–4 (223, 47)
26	Table IV		(2) K/PΘ	K/K 0–3, KΘ/KΘ 0–2, P/P 0–2, PΘ/PΘ 0–4 (225, 238)
27	Table IV		(2) CofΘ/S	Cof/Cof 0–2, CofΘ/CofΘ 0–5, S/S 0–3, SΘ/SΘ 0–2.
28	Table IV		EΘ/S	EΘ/EΘ 0–1, (231)
29	Table IV		(2) Jsf/Ksf	Ksf/Ksf 0–4, Jsf/Jsf 0–1 (239, 240)
30	Table IV	(+/+)	× Hm/K	K/K 0–7, Hm/Hm 0–1
31	Table IV		H/F	H/H 0–1–1, F/F 0–1
32	Bis. 205–7	(CofΘ/E)	× H/K	H/H 0–2, K/K 0–2
33	Dir. 12	(Cof/S)	× HmΘ/HmΘ	HmΘ/HmΘ 0–6 (214, 215)
34	Dir. 12	(K/Sm)	× HmΘ/HmΘ	HmΘ/HmΘ 0–12 (216)

TABLE II. (*Continued*).

Items.	Source.	Males.	Females.	Offspring.
35	Dir. 22		Jsf/Jsf	Jsf/Jsf 0–2
36	Dir. 35	(B/KΘ)	× Jsf/Jsf	Jsf/Jsf 0–1 (217)
37	Bis. 203–6		Cof/I	Cof/Cof 0–7–1, I/I 0–9 (208, 38, 39) (Later mated to ♂ EΘ/K and produced Cof/K 0–1)
38	Dir. 37		Cof/Cof	Cof/Cof 0–3 (Same ♀ later mated 243, Table V)
39	Dir. 37		Cof/Cof	Cof/Cof 0–3
40	Bis (1) 208–37 Bis. (4) 202–4	(KΘ/L)	× B/E	B/B 0–2, E/E 0–3, (220, 221)
41	Bis. 204–6		(2) CofΘ/S	Cof/Cof 0–8, CofΘ/CofΘ 0–22, S/S 0–13, SΘ/SΘ 0–13 CofΘ/S(Θ ?) 0–1, Cof/CofΘ 0–1 (229, 230, 244, 245).
42	Bis. 204–6		(2) KΘ/S	K/K 0–11, KΘ/KΘ 0–11, S/S 0–10, SΘ/SΘ 0–17, (234, 235, 236, 237)
43	Bis.(1)229–41 Bis.(1)235–42		EΘ/S	E/E 0–3, EΘ/EΘ 0–1, SΘ/SΘ 0–1
44	Bis.(1)229–41 Bis(4)202–4 Bis.(1)235–42	(B/JofΘ)	× Cof/K	Cof/Cof 0–1, K/K 0–3 (218, 219)
45	Bis.212–12 Bis.(3)204–6	(SΘ/S_1)	× Hm/K	K/K 0–1
46	Bis.215–33	(+/+)	× Cof/HmΘ	Cof/Cof 0–2, CofΘ/CofΘ 0–1, HmΘ/HmΘ 0–2 (222)
47	Dir. 25	(CofΘ/K)	× H/H	H/H 0–3
48	Bis.(5)202–4	(F/J)	× EΘ/Ksf	KΘsf/KΘsf 0–1
49	Bis.(2)208–37 Bis.(5)202–4 Bis(2)235–42	(Cof/KΘ)	× Jsf/Psf	Jsf/Jsf 0–8, Psf/Psf 0–10
50	Bis.(5)202–4 Bis.(2)235–42 Bis.(2)208–37	(H/S_1)	× KΘsf/Psf	Ksf/Ksf 0–1, KΘsf/KΘsf 0–1, PΘsf/PΘsf 0–1
51	Bis.(1)205–7		B/K	B/B 0–3–1, K/K 0–4 (224)
52	Bis.(2)226–76 Bis.(3)211–12 Bis.(4)208–37 Bis.(2)224–51 Bis.(6)202–4 Bis.(4)235–42	(I/S_1Θ)	× B/K	B/B 0–3, K/K 0–5
53	Many, La., 1925 Bis.(2)233–20 Bis.(2)235–42		(2) +/KΘ	+Θ/+Θ 0–1

TABLE II. (*Continued*).

Items.	Source.	Males.	Females.	Offspring.
54	Bis. 205–7		(2) B/H	H/H 0–1
55	Bis.(1)205–7		B/H	B/B 0–4, H/H 0–7 (60)
56	Bis.(1)205–7		B/H	H/H 0–1
57	Bis.(1)205–7		B/H	B/B 0–2, H/H 0–4
58	Bis.(1)205–7		B/K	K/K 0–1
59	Bis.(1)205–7		B/K	B/B 0–2
60	Dir. 55		(2) H/H	H/H 0–13
61	Bis. 205–7		(2) H/K	H/H 0–15, K/K 0–4 (246)
62	Bis.(1)205–7		H/K	H/H 0–1, K/K 0–1
63	Bis.(1)205–7		H/K	H/H 0–2, K/K 0–2
64	Bis.(1)205–7		H/K	H/H 0–5 (232, 248)
65	Bis.(5)202–4		(2) Cof/EΘ	CofΘ/CofΘ 0–1
66	Bis.(1)233–20 Bis.(1)236–42		(2) CofΘ/E	Cof/Cof 0–1, E/E 0–1
67	Bis.202–4		Cof/K	Cof/Cof 0–0–4, K/K 0–4 (228)
68	Bis.204–6		(2) Cof/S	Cof/Cof 0–5, S/S 0–5
69	Bis.(1)203–6 Bis.228–67		E/K	E/E 0–3, K/K 0–3
70	Bis.(3)202–4 Bis.208–37		I/KΘ	I/I 0–1
71	Bis.(1)209–12		(2) H/KΘ	H/H 0–1, HΘ/HΘ 0–2, K/K 0–1, KΘ/KΘ 0–2
72	Bis.(1)208–37 Bis.(3)202–4		(2) I/K	K/K 0–1
73	Bis. 204–6		(2) K/S	K/K 0–8, S/S 0–10
74	Bis. 204–6		(2) K/S	K/K 0–1, S/S 0–3
75	Bis.(4)202–4 Bis.(1)208–37		LΘ/M	L/L 0–6, LΘ/LΘ 0–4, M/M 0–2, MΘ/MΘ 0–2
76	Dir. 20		M/M	M/M 1–1 (226, 226a)
77	Many, La., 1925 Bis. 222–46		(2) HmΘ/L	LΘ/LΘ 0–1 (78)
78	Dir. 77		LΘ/LΘ	LΘ/LΘ 0–24 (241, 242)
79	Bis.(2)204–6	(EΘ/M)	× Cof/K	K/K 0–1, Cof/Cof 0–1
80	Bis. 213–13		(2) Jsf/KΘsf	Jsf/Jsf 0–3, JΘsf/JΘsf 0–1, Ksf/Ksf 0–1
81	San. Ant., 1926 Bis.(3)213–13 Bis.(4)208–37	(+/+)	× EΘ/L	E/E 0–2, EΘ/EΘ 0–1, L/L 0–2, LΘ/LΘ 0–2
82	Sugarland, 1926 Bis(8)202–4 Bis.(4)213–13		(2) + Φ/PsfΘ	+ ΘΦ/+ ΘΦ 0–3, + Θsf/+ Θsf 0–1, + Φ/+ Φ 0–1, Psf/Psf 0–2, PΘsf/PΘsf 0–1
83	Sugarland, 1926 Bis.(8)202–4 Bis.(4)213–13		B/PΘsf	BΘ/BΘ 0–1, Psf/Psf 0–1, PΘ/PΘ 0–1

and 6, having lost them in the several bisexual generations (on record, but not essential to this inquiry) through which her ancestry had passed.

In a few cases the ancestries of parthenogenetic females trace back, through biparental breeding, to two, item 40, et al., three, items 44, 49, 50, or six, item 52, different parthenogenetic progenitresses.

Explanation and Illustration of the Use of Table III.—These are simple matings with the progeny showing preponderantly participation of the males in the parentage. However, one to seven individuals of each mating did not show any of the color characters of the male members of the matings, and all such were females. Since the dominant characters of the males, according to all experience, were due to show in any possible biparental progeny, these aberrant individuals are thought to have developed from unfertilized eggs.

The sources are to be read in the same way as in Table II. The ancestry of the females, only, is traced. Example, mating 101: The regions in nature from which the progenitors of the female B/S_1 came may be noted in Table IV., item 101. She had no parthenogenesis in her recorded progenitorship. Example, mating 110: The ancestry of the female parent, B/K, goes back to a progenitor, each, from Many, La., 1925, and Sugarland, Texas, 1926 (Neither of these is shown in Table IV.). Her line also goes back through six bisexual generations, not included in these data, through mating 202, Table V., to the parthenogenetic female of item 4, Table II., indicated by the Bis.(6)202–4. The Bis. (3) 235–42 means that the ancestry of this female, B/K, also goes back through three bisexual, Bis., generations, not included in the tables, to mating 235, Table V., to the parthenogenetic female of item 42, Table II.

Explanation and Illustration of the Use of Table IV.—In this table are denoted the males and females secured at various places, over a period of years, which constituted the progenitorship from nature of the 47 females, items 1–31, Tables II. and IV., and matings 100–106, Tables III. and IV., which first gave offspring parthenogenetically. The lines of ancestry of all the other 68 parthenogenetic females, Table II, and the other eight of Table III., in turn, extend back to some of these.

TABLE III.

MATINGS THAT GAVE SOME PARTHENOGENETIC INDIVIDUALS.

Mating Number.	Source.	Parents.	Offspring.
100	Table IV	P/P × +/KΘ	+/P 7–14, +Θ/P 6–12, K/P 9–12, KΘ/P 5–13, +/+ 0–2, K/K 0–1, KΘ/KΘ 0–1
101	Table IV	F/HΘ × B/S_1	B/F 1–2, B/FΘ 3–1, B/H 1–1, B/HΘ 0–1, F/S_1 2–5, FΘ/S_1 0–1, H/S_1 0–3, HΘ/S_1 2–0, B/B 0–2, S_1/S_1 0–5
102	Table IV	J/K × Cof/SmΘ	Cof/J 4–6, CofΘ/J 2–2, Cof/K 2–1, CofΘ/K 3–1, J/Sm 3–3, J/SmΘ 2–2, K/Sm 3–5, K/SmΘ 1–2, Sm/Sm 0–1
103	Table IV	CofΘ/Sm × J/P	CofΘ/J 1–1, CofΘ/P 1–0, J/Sm 4–1, J/SmΘ 0–1, P/Sm 0–2, P/SmΘ 0–1, J/J 0–1
104	Table IV	E/K × B/I	B/E 1–2, B/K 1–3, E/I 3–1, I/K 3–1, B/B 0–1
105	Table IV	Cof/K × B/JΘ	B/K 8–12, BΘ/K 5–7, J/K 4–6, J/K 2–5, JΘ/K 5–5, JΘ/K 5–3, B/Cof 11–9, BΘ/Cof 7–7, Cof/J 6–4, Cof/JΘ 12–8, BΘ/BΘ 0–1
106	Table IV	P/S × CΘ/K	C/P 0–1, KΘ/S 0–1, CΘ/S 0–1, C/S 1–0, CΘ/CΘ 0–1
107	Bis.(1)208–37 Bis.(2)202–4	B/M × IΘ/K	B/I 5–6, B/IΘ 4–4, B/K 3–2, B/KΘ 3–2, I/M 4–3, IΘ/M 3–6, K/M 4–5, KΘ/M 4–3, K/K 0–1
108	Many, La., 1925 Bis.(1)233–20	Cof/KΘ × +/M	+/Cof 4–1, +/K 1–0, +/KΘ 2–2, Cof/M 3–4, CofΘ/M 0–1, K/M 0–1, KΘ/M 3–2, M/M 0–1
109	Bis.(5)202–4 Bis.(2)208–37 Bis.(2)235–42	I/LΘ × Cof/Sm	Cof/I 9–1, Cof/IΘ 1–1, Cof/L 2–1, Cof/LΘ 4–3, I/Sm 3–2, IΘ/Sm 1–3, L/Sm 0–2, LΘ/Sm 4–0, Cof/Cof 0–1
110	Many, La., 1925 Sugarland, 1926 Bis.(6)202–4 Bis.(3)235–42	C/P × B/K	B/C 1–0, B/P 0–3, C/K 3–0, K/P 0–2, K/K 0–1
111	Bis.(7)202–4	D/S_1Θ × H/K	D/H 1–5, DΘ/H 0–2, D/K 1–3, H/S_1 3–8, H/S_1Θ 1–2, K/S_1 1–3, K/S_1Θ 4–2, H/H 0–1
112	Bis.(3)210–12	BΘ/Sm × +/Jof	+/BΘ 0–1, +/Sm 1–0, BΘ/Jof 1–0, Jof/Sm 1–0, +/+ 0–1, Jof/Jof 0–3
113	Bis.(4)209–12 Bis.(7)202–4 Bis.(5)208–37	BΘ/I × Jof/L	B/Jof 3–9, BΘ/Jof 15–7, B/L 7–4, BΘ/L 9–6, I/Jof 10–9, IΘ/Jof 9–2, I/L 12–8, IΘ/L 6–3, Jof/Jof 0–1
114	Bis.(2)202–4	B/B × H/SΘ	B/H 11–7, B/HΘ 7–7, B/S 10–7, B/SΘ 18–7, H/H 0–1

The abbreviations, in the first column, are as follows: B.R. '10, Baton Rouge, La., 1910; Many, La., 1909, 1911, 1914; Mac. '17, Mackay, Texas, near Wharton, 1917; Bea. '17, '18, Beaumont, Texas, 1917, 1918; C.S. '21, College Station, Texas, 1921; Sug. '13, '21, '22, Sugarland, Texas, 1913, 1921, 1922; Hou. '08, '11, etc., Houston, Texas, 1908, 1911, 1913, 1914, 1916, 1918, 1921, 1922; Aus. '21, '22, '23, Austin, Texas, 1921, 1922, 1923; S.A. '11, '24, San Antonio, Texas, 1911, 1924. Tables II. and III., at the bottom reading to the right, refers to the items 1–31, Table II and matings 100–106, Table III. The column of small letters above each of these indicates the number of ancestors, male or female, or both, from each place and date. Items 15, 25, in the thirteenth column, 18, 27, 28, in the sixteenth, and 23, 26, 29 and mating 103, in the twenty-third column, had the same progenitorship, respectively.

Reading from left to right, the same letters, after a place and date, denote the same individuals. Examples: The small letters, a-d, repeated 29 times, after B.R. '10, means that four individuals, males or females, or both, named a, b, c and d, respectively, collected at Baton Rouge, La., in 1910, were ancestors from nature of all, except those of the last three columns, items 2, 10 and 31. Reading to the right of Hou. '14, there were 13 individuals, a, b, c, d, e, f, g, h, i, j, k, l and m (a-m) which were in the line of descent of all except the last three, items 2, 10 and 31. Reading up from item 22, there were 71 progenitors of this female from nature; two, a and b, from S.A. '11; ten, a-d, k, l, o, p, w and x, from Aus. '22; seven, a-g, from Aus. '21; one, c, from Hou. '22; one, a, each from Hou. '21 and Hou. '18 and so on up to the top where four, a-d, were from B.R. '10. From Aus. '21, item 6 had c, d, e, f and g (c-g); item 104 had e, f, g (e-g); item 1 and mating 106 had the same four, c, d, e, f (c-f); item 3 had two, e and f, of these; all others, except items 2, 10 and 31 had these four, c-f, and, in addition, a, b and g (a-g) in their lines. The largest number of progenitors, 26 in all, was from Austin, 1922. Items 1, 4, 5, 10, and 31, are clear of these; one, y, contributed to the progenitorship of item 2, and the largest contribution, a-g, i-p, s-v and z, 20 in all, was to the female of mating 105.

Item 2 had one progenitor from Sug. '22, 2 from Hou. '22 and

TABLE IV.

WHERE PROGENITORS OF PARTHENOGENETIC INDIVIDUALS WERE COLLECTED (EXPLANATION IN TEXT).

B.R. '10	a-d	a-d	a-d	a-d	a-d	a-d	a-d	a-d	a-d	a-d	a-d	a-d	a-d	a-d	a-d	a-d	a-d	a-d	a-d	a-d	a-d	a-d	a-d	a-d	a-d	a-d	a-d	a-d	a-d	a-d				
Many '09	a,b	a,b	a,b	a,b	a,b	a,b	a,b	a,b	a,b	a,b	a,b	a,b	a,b	a,b	a,b	a,b	a,b	a,b	a,b	a,b	a,b	a,b	a,b	a,b	a,b	a,b	a,b	a,b	a,b	a,b				
Many '11	a,b	a,b	a,b	a,b	a,b	a,b	a,b	a,b	a,b	a,b	a,b	a,b	a,b	a,b	a,b	a,b	a,b	a,b	a,b	a,b	a,b	a,b	a,b	a,b	a,b	a,b	a,b	a,b	a,b	a,b				
Many '14	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a				
Mac. '17		a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a				
Bea. '17	a,b	a,b	a,b	a,b	a,b	a,b	a,b	a,b	a,b	a,b	a,b	a,b	a,b	a,b	a,b	a,b	a,b	a,b	a,b	a,b	a,b	a,b	a,b	a,b	a,b	a,b	a,b	a,b	a,b	a,b				
Bea. '18	b,c	b-e	b-e	b-e	b-e	b-e	b-e	b-e	a-e	a-e	a-e	a-e	a-e	a-e	a-e	b-e	b-e	a-e	a-e	b-e	b-e	a-e	a-e	b-e	a-e	a-e	a-e	b-e	a-e	b,c				
C.S. '21	b		b	a,b	a	b	a,b	a,b	a,b	a,b	a,b	a,b	a,b	a,b	a,b	a,b	a,b	a,b	a,b	a,b	a,b	a,b	a,b	a,b	a,b	a,b	a,b	a,b	a,b	a,b				
Sug. '13	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a				
Sug. '21	b,c	b,c	b,c	a-c	a-c	b-c	a-c	a-d	a-d	a-d	a-d	a-d	a-d	a-d	a-d	a-c	a-c	a-d	a-d	a-c	a-c	a-d	a-d	a-c	a-d	a-d	a-d	b,c	a-d	a-c				
Sug. '22				d,e h		f,g	c-e	d-g i	d-g	d-g i	c-i	d-g i	a-i	a-g i	a,b d,i	c-e h,i	d,e i	d,e i	c-e i	c-e	d-g j	d-g j	c-h	a-g j	a-i	a-i	c	a-i	d,e	c				
Hou. '08	a,b	a,b	a,b	a,b	a,b	a,b	a,b	a,b	a,b	a,b	a,b	a,b	a,b	a,b	a,b	a,b	a,b	a,b	a,b	a,b	a,b	a,b	a,b	a,b	a,b	a,b	a,b	a,b	a,b	a,b				
Hou. '11	a,b	a,b	a,b	a,b	a,b	a,b	a,b	a,b	a,b	a,b	a,b	a,b	a,b	a,b	a,b	a,b	a,b	a,b	a,b	a,b	a,b	a,b	a,b	a,b	a,b	a,b	a,b	a,b	a,b	a,b				
Hou. '13	a,b	a,b	a,b	a,b	a,b	a,b	a,b	a,b	a,b	a,b	a,b	a,b	a,b	a,b	a,b	a,b	a,b	a,b	a,b	a,b	a,b	a,b	a,b	a,b	a,b	a,b	a,b	a,b	a,b	a,b				
Hou. '14	a-m	a-m	a-m	a-m	a-m	a-m	a-m	a-m	a-m	a-m	a-m	a-m	a-m	a-m	a-m	a-m	a-m	a-m	a-m	a-m	a-m	a-m	a-m	a-m	a-m	a-m	a-m	a-m	a-m	a-m				
Hou. '16	a-e	a-e	a-e	a-e	a-e	a-e	a-e	a-e	a-e	a-e	a-e	a-e	a-e	a-e	a-e	a-e	a-e	a-e	a-e	a-e	a-e	a-e	a-e	a-e	a-e	a-e	a-e	a-e	a-e	a-e				
Hou. '18	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a				
Hou. '21	a		a	a		a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a				
Hou. '22					a,b f	d,f	c	d,f	d	a,b d,f	a-d f	a,b d,f	a-d f	a-d f	d,f	a-d f	a,b f	a,b f	a-d c	a,b d,f	a,b d,f	c,d	a-d f	a-d f	a-d f	c,f	a-d f		c,e				
Aus. '21	c-f	e,f	a-g	a-g	c-g	a-g	a-g	a-g	a-g	a-g	a-g	a-g	a-g	a-g	a-g	a-g	a-g	a-g	a-g	a-g	a-g	a-g	a-g	a-g	a-g	a-g	a-g	c-g	a-g	c-f				
Aus. '22		i,j e,t			h q,r	i,j s,t	a-d k,l o,p w,x	i-l o,p z	k,l o,p z	e,f i-l o,p	h-l o-r w,x	e-f h,k l o-r z	e-l o-x z	a-g i-l, o,p s-x	a-d g i-p s-v	e-g i-l o,p s,t w,x z	e,f h-l q-t	e,f h,k l q-t	a-f k,l o,p w,x	a-d k,l o,p w,x	e,f i-p s,t	e,f i-l o,p	a-d i-l o,p w,x	a-g i-l o,p s-x	e-p s-x z	e-l o-x z	i,j w,x	a-g i-p s-v z	g i,j	y			
Aus. '23								c,d	c,d	e		c-e	a-e	a,b e	a,b				c,d		e	e		a,b	c,d	a-d		a-d					
S.A. '11	a,b	a,b	a,b	a,b	a,b	a,b	a,b	a,b	a,b	a,b	a,b	a,b	a,b	a,b	a,b	a,b	a,b	a,b	a,b	a,b	a,b	a,b	a,b	a,b	a,b	a,b	a,b	a,b	a,b	a,b				
S.A. '24									a			l	l	c-f							b g-k o,p			c-f	g,h m,n q,r					q,r			New Braunfels, 1926.
Items & Matings Tables II & III	1	3	4	5	6	7	8	9	11	12	13	14	15 25	16	17	18 27 28	19	20	21	22	24	30	23 26 29 103	100	101	102	104	105	106	2	10	31	

one from Aus. '22. The parent in item 10 came directly from a pair from S.A. '24, and 31 from a pair from New Braunfels, Texas, 1926.

This is a most intricate and, perhaps, formidable table into which many pages of writing have been condensed, but, with the aid of the references in Tables II., III. and V., one may trace the progenitorship of every parthenogenetic individual, either directly, or through one or more parthenogenetic lines, to nature where and when it became possible to begin the records.

Explanation and Example of the Use of Table V.—The second column shows the sources, in Table II., of the parthenogenetically derived females of these matings. The matings represented in this table constitute tests of the homozygosity of these females, and of the one male, matings 226, 226a. Mating 215, Table V., gave one offspring without the · for which the female parent was supposed to be homozygous. One individual, the female of mating 229, proved to be heterozygous for a factor. These cases will be reviewed in the discussion section.

Example 204: The female S/S was of the parthenogenetic progeny of item 6, Table II. The figures 41, 42, 68, 73 and 74 indicate that females from these bisexual progeny may be found to have repeated the parthenogenesis of their grandmother in the respective items, 41, 42, etc., Table II. The formula (2)79, means that some of these progeny were bred bisexually for two generations (not included in these tables) and then one of the females reproduced parthenogenetically, item 79, Table II. The last figures, (3)45 show that some of these progeny were bred three bisexual generations (not shown here), probably being mated with unrelated stocks, and then one of the females produced parthenogenetically, item 45, Table II.

Examples, matings 209–212: The females were all of the parthenogenetic progeny of item 12, Table II. The figures, in parentheses, at the right, show that some of these progeny were bred, one in 209, through one, (1) 71, bisexual generation and then two of the females used in parthenogenesis, item 71, Table II.; another one on 209, through four, (4) 113, bisexual generations to mating 113, Table III.; the one in 210, through three, (3) 112, bisexual generations to mating 112, Table III; the one in 211

TABLE V.

TESTING PARTHENOGENETICALLY PRODUCED INDIVIDUALS.

No.	Source of Female.	Parents.	Offspring.
200	3	JΘ/K × B/B	B/JΘ 1–0
201	4	K/PΘ × Cof/Cof	Cof/KΘ 1–0, Cof/PΘ 0–1
202	4	EΘ/K × Cof/Cof	Cof/E 0–1, Cof/EΘ 3–2, Cof/K 6–4, Cof/KΘ 2–1 67, (2) 115, (3) 70, 72, (4) 40, 44, 75, 107, (5) 48, 49, 50, 65, 109, (6) 52, 110, (7) 111, 113, (8) 82, 83, 114
203	6	Cof/E × I/I	E/I 4–4, Cof/I 7–8 37, (1) 69
204	6	CofΘ/K × S/S	Cof/S 2–2, CofΘ/S 7–4, K/S 5–8, KΘ/S 1–2 41, 42, 68, 73, 74, (2) 79, (3) 45
205	7	B/K × H/H	B/H 4–3, H/K 5–6, 32, 54, 61, (1) 51, 55, 56, 57, 58, 59, 62, 63, 64, (7) 114.
206	8	I/K × J/J	I/J 2–1
207	10	K/SΘ × C/C	C/K 0–2
208	37	K/LΘ × I/I	I/K 18–13, I/KΘ 6–5, I/L 6–3, I/LΘ 17–9, I/I 0–1, 70, (1) 40, 72, 75, 107, (2) 49, 50, 109, (3) 52, (4) 81, (5) 113
209	12	KΘ/N × M/M	NΘ/M 1–4, K/M 2–0, KΘ/M 5–5, N/M 3–3, (1) 71, (4) 113
210	12	Jof/Jof × MΘ/MΘ	Jof/MΘ 1–1, (3) 112
211	12	K/LΘ × Hm/Hm	Hm/LΘ 2–0, Hm/K 0–1, Hm/KΘ 0–1, (3) 52
212	12	CofΘ/K × Hm/Hm	Hm/K 3–3, Hm/KΘ 0–1, CofΘ/Hm 1–1, (1) 45
213	13	KΘ/P × J/J	J/KΘ 3–7, J/P 3–2, J/PΘ 2–2, J/K 5–2, (1) 80, (3) 81, (4) 82, 83
214	33	B/K × HmΘ/HmΘ	B/HmΘ 3–4, HmΘ/K 5–3
215	33	Cof/K × HmΘ/HmΘ	HmΘ/K 27–14, Cof/HmΘ 24–18, Cof/Hm 1–0, (1) 46, (3) 114
216	34	E/S × HmΘ/HmΘ	E/HmΘ 2–1, HmΘ/S 2–2, HmΘ/HmΘ 0–1
217	36	KΘ/P × Jsf/Jsf	Jsf/K 4–2, Jsf/KΘ 10–8, Jsf/P 14–9, Jsf/PΘ 7–3
218	44	Cof/EΘ × K/K	Cof/K 1–0, CofΘ/K 2–0, E/K 1–0, EΘ/K 4–1
219	44	Cof/EΘ × K/K	E/K 1–0, EΘ/K 3–1
220	40	JΘ/K × B/B	B/J 1–1, B/JΘ 1–5, B/K 1–5, B/KΘ 0–1 (2) 114
221	40	J/KΘ × E/E	E/J 4–5, E/JΘ 1–1, E/KΘ 4–3
222	46	L/Sm × HmΘ/HmΘ	HmΘ/L 2–3, HmΘ/Sm 2–4 77
223	25	B/CofΘ × H/H	B/H 1–3, CofΘ/H 1–0

TABLE V. (*Continued*).

No.	Source of Female.	Parents.	Offspring.
224	51	I/KΘ × B/B	B/KΘ 0–2, B/IΘ 0–2 (2) 52
225	26	B/S × PΘ/PΘ	B/PΘ 6–10, PΘ/S 4–6
226	76	M/M × Cof/L	L/M 13–6, Cof/M 15–11 (2) 52
226a	76	M/M × B/K	B/M 15–15, K/M 23–14
227	21	CofΘ/E × K/KΦΦ	Cof/KΦ 1–0
228	67	E/I × K/K	E/K 4–3, I/K 8–3 69
229	41	K/S × Cof/CofΘ	Cof/K 2–3, Cof/S 6–6, CofΘ/K 6–3, CofΘ/S 4–5 (1) 43, 44
230	41	+/Jof × SΘ/SΘ	+/SΘ 5–1, Jof/SΘ 2–4
231	28	K/N_1 × EΘ/EΘ	EΘ/K 0–1
232	64	CofΘ/K × H/H	Cof/H 0–1, CofΘ/H 2–4, H/KΘ 2–0
233	20	CofΘ/E × M/M	E/M 11–10, EΘ/M 8–2, Cof/M 9–6, CofΘ/M 12–9 (1) 66, 108, (2) 53, (5) 114
234	42	Cof/EΘ × S/S	Cof/S 3–0, CofΘ/S 1–0, E/S 1–2, EΘ/S 7–2
235	42	EΘ/L × K/K	E/K 2–3, EΘ/K 7–5, K/L 13–8, K/LΘ 1–0 (1) 43, 44, (2) 49, 50, 53, 109, (3) 110, (4) 52
236	42	CofΘ/E × K/K	E/K, +EΘ/K 7–5, Cof/K 6–3, CofΘ/K 4–2 (1) 66
237	42	B/H × SΘ/SΘ	B/SΘ 15–13, H/SΘ 10–14 (5) 114
238	26	BΘ/Hm × K/K	B/K 1–0, BΘ/K 2–1, Hm/K 1–3, HmΘ/K 1–0
239	29	K/LΘ × Ksf/Ksf	Ksf/K 0–2, Ksf/L 1–0
240	29	+/SΘ × Jsf/Jsf	+/Jsf 2–4, Jsf/S 1–0, Jsf/SΘ 6–3
241	78	C/S_1 × LΘ/LΘ	C/LΘ 1–0
242	78	C/S_1 × LΘ/LΘ	C/LΘ 2–1, LΘ/S_1 0–2
243	37	JΘ/K × Cof/Cof	Cof/J 7–4, Cof/JΘ 15–7, Cof/K 6–8, Cof/KΘ 6–4
244	41	M/Sm × CofΘ/CofΘ	CofΘ/Sm 1–1, CofΘ/M 2–1
245	41	I/K × Cof/Cof	Cof/I 2–5, Cof/K 6–1
246	61	I/LΘ × K/K	I/K 0–1, IΘ/K 0–1, K/LΘ 0–1
247	12	Cof/K × MΘ/MΘ	K/MΘ 3–5, Cof/MΘ 6–0
248	64	CofΘ/K × H/H	CofΘ/H 1–0, H/K 1–1, H/KΘ 1–2, Cof/H 0–1
249	17	Cof/K × F/F	Cof/F 1–0

through three, (3) 52, bisexual generations to item 52, Table II., and the one in 212 through one, (1) 45, bisexual generation to item 45, Table II., respectively.

Discussion.

The comparatively sudden inception of a considerable degree of parthenogenesis in *P. texanus,* beginning in 1922, after fourteen years of perhaps exclusively bisexual reproduction, implied the recent introduction, prior to this date, of some causative factor, or factors. Then came the proposals of Peacock and Harrison (1925, 1926): (1) The generalization, deduced largely from the results of their own experiments, *that parthenogenesis was consequent upon hybridity,* and, (2) from my data, that the rather extensive parthenogenesis exhibited by *A. eurycephalus* (Nabours, 1919, 1925) was the result of hybridizing one variety of this species from Tampico, Mexico, with another from the region of Houston, Texas.

In 1921, the year preceding the onset of this period of parthenogenesis in *P. texanus,* specimens had been secured at Austin and College Station, Texas, new areas along the northeastern boundary of the range of the species (Table IV.). It was noted that all the parthenogenetic individuals, 1922–1926, had in their ancestry progenitors from these new areas, except that those of item 3, Table II. and IV., did not connect with College Station. Item 2, Table II. and IV. had one ancestor from Austin, 1922. The females of items 10 and 31 were from parents collected at San Antonio, 1924, and New Braunfels, 1926, respectively.

The arrangements of the data in the tables, especially Table IV., have been influenced by these considerations. The ancestry of all the parthenogenetic individuals may be traced to their various origins in nature. The 40 females of items 1–31, Table II., and 7 of matings 100–106, Table III., had no recorded parthenogenetic progenitresses; the other 68 females of Table II., and 8 females of Table III., in turn, were descendants of these.

An examination of Table IV. reveals a very complex ancestry for these 47 females which first displayed this characteristic, and from which all the other parthenogenous ones were descended. But it appears to have remained for the introduction of the speci-

mens from Austin, 1921, to bring in the factor, or *the complementary climaxing factor, or factors,* responsible for the significant measure of parthenogenesis which ensued.

However, possibly opposing this tentative suggestion were the two cases of parthenogenesis, items 10 and 31, Table IV., directly from San Antonio and New Braunfels (about half way between San Antonio and Austin), respectively. The female of item 2, Tables II., and IV., had few recorded progenitors, but one of them was from Austin, 1922. It is difficult to estimate the importance of the three cases of probable parthenogenesis of 1912 and 1915 (see pp. 130, 131).

The narrow confines of Shoal Creek, near Austin, is the only new area that contributed to the progenitorship of all the parthenogenetic females, except items 10 and 31, beginning in 1921. The female of 10 was from San Antonio, but taken 13 years after the two original progenitors (Table IV.). The female of item 31 was from New Braunfels, which was also a new area, near Austin. The factor, or factors responsible for parthenogenesis may even have been contributed from Houston, or Sugarland, 1922, the several previous collections from these areas having possibly simply missed the parthenogenetic strain, if such there was.

It was urgent that a strain highly parthenogenous should be hybridized with one which was not so at all, and then the causative factors recovered. A few such experiments have been attempted, the least unsatisfactory one having been conducted as follows: The male B/K, mating 205, Table V., had no parthenogenesis in his recorded ancestry. The female, H/H, was a parthenogenetic product, item 7, Table II. They gave bisexually both males and females in F_1. Eight of the nine female F_1 progeny were disposed of as follows: Four unmated, two in one cage and two in another, gave offspring, items 54, 61, Table II. (obviously one of those in 54 did not reproduce). Three were mated out; one gave no offspring, one gave bisexual (not included in the tables) and the other parthenogenetic progeny, item 32, Table II. The eighth female was mated to a brother and they gave a numerous F_2 progeny (not included in tables). From these F_2 (parthenogenetic by nonparthenogenetic?) progeny, eighteen females were separated, one each, in cages; nine gave offspring, and two

others were known to have laid a batch of eggs each which were not given opportunity to hatch, items 51, 55–59, 62–64, Table II. Some of the other seven may have laid eggs, but they did not reproduce. The quantitative results of this experiment thus appeared to constitute a superb and convincing case of parthenogenesis as a dominant Mendelian characteristic.

However, the following facts concerning the conditions of the experiment should be taken into consideration: Five of the F_2 females, the first to become adult, had been placed in their respective cages on May 23; the other 13 had been placed on June 14, twenty-two days later, that much farther on into the hot summer, and past the optimum breeding season which was March–May (See Table I.). The records show that the five placed first all gave progeny of 3, 9, 17, 17, and 20, respectively. Only three of the 13 females, placed 22 days later, gave offspring, two hatching one each, and the other, five. As noted above, at least two others laid batches of eggs. The question is still open: What would have been the result if all eighteen of these F_2 females had been placed May 23 or earlier? Or, what would have happened if all of them had been placed on June 14, or later?

All the females and one male of *A. eurycephalus* hatched from unfertilized eggs, which were tested by further breeding, proved to be homozygous for all the observable characteristics. Obviously, it could not be stated categorically that any of the untested ones were homozygous since the color patterns were dominant (Nabours, 1919, 1925). The females and one male of *P. texanus,* so far as they were tested, were also homozygous, except that one individual of item 41, Table II., had the appearance of having both the alternatives Cof and S, and another also from 41, was proved to be heterozygous for ♀, mating 229, Table V. Mating 215, Table V., contained one Cof/Hm, the only one in 84 without the ♀ for which the female parent was supposed to be homozygous. Cof and S are certainly very closely linked, if not precisely alternative; so it is unlikely that there was crossing over. The failure to breed this animal leaves the question of her actual genetic composition in obscurity. About the Cof/Cof♀ individual, there was only the question of the cause. The factor for ♀ appears to be near the end of the chromosome (Haldane, 1920).

As is shown by W. R. B. Robertson (MSS, 1929, Nabours, 1929), the homologous chromosomes of the germ and somatic cells of the parthenogenetic offspring have a tendency to lie together in pairs, often even adhering, so that a pair may appear as one, double in size. Pending further developments, it may be suggested that these aberrances were brought about through, perhaps, an adherance, in the one case, and an elimination of the ends of the chromosomes containing θ, in the others.

The inheritance results in parthenogenesis indicate that segregation and crossing over occur before the inception of the parthenogenetic processes, and that up to this stage in gametogenesis there is no essential departure from the usual procedure in bisexual reproduction (Nabours, 1925, 1929).

Dr. W. R. B. Robertson, working in our laboratory, has discovered that the numbers of chromosomes in some of the soma cells, likewise the oögonial cells, of the parthenogenetically produced females of *A. eurycephalus* and *P. texanus* appear to range from seven to fourteen, though there are actually fourteen in all of them. When the full fourteen are manifest, the members of the homologous pairs, respectively, lie together in early cell division, and not far apart, each from the other in later cell generations, in such positions as to suggest the second polar body division had been inhibited.

When only seven chromosomes appear to be present in these parthenogenetically produced individuals, *each has twice the bulk in transverse thickness (broadness of the equatorial plane) of either member of the similarly numbered pair in the cells containing seven discreet pairs.* Furthermore, in these parthenogenetically produced grouse locusts, Robertson notes that in those soma and oögonial cells *containing above seven chromosomes, there is one less of the broad chromosomes for every additional one above seven.* For example, if the *apparent* number is nine, there are five of double equatorial broadness, or bulky ones, and four smaller ones in two pairs, the homologues of which always lie together, or not far from each other, in the same manner as the similar pairs do in those cells of the parthenogenetically derived females containing the fourteen discreetely paired chromosomes. An analogous situation is found in the cells of the parthenogeneti-

called derived males which he has examined (Robertson, 1929, MSS., Nabours, 1929).

The entrance of the sperm is probably necessary to the second polocyte division in the *Tettigidae* (loc. cit.), as in other forms, another "case of a later stage of maturation being overlapped by an earlier stage of fertilization" (Wilson, 1925). Fertilization lacking, there is a resultant partial or complete inhibition of the last polocyte division which restores or retains the condition of diploidy (See Robertson's observations on the chromosomes pp. 151, 152 and in MSS., and Nabours, 1929). When the specific gene or complementary genes responsible for parthenogenesis are present, development is initiated. As already stated (pp. 131, 132), probably no female would be partheno-producing if mated with a potent male (those not carrying the specific genes probably require fertilization). Therefore such initiation of development as this might, in effect, be termed *artificial* parthenogenesis.

The kind of parthenogenesis shown by the grouse locusts can hardly be called *facultative,* and certainly not *obligatory* (See definitions, Wilson, 1925, pp. 228, 229). It might perhaps be best entitled *tychoparthenogenesis,* and preponderantly *gynogenetic.*

In a parthenogenetic line of *P. texanus,* a female exposed to a male gave parthenogenetic progeny. Seven of these were mated out; five gave biparental offspring, but the other two again gave parthenogenetic progeny in spite of the males to which they had been exposed. However, the progeny of the second parthenogenetic generation, when exposed to males, mated and gave offspring from fertilized eggs (items 12, 33, 34, Table II., and matings 209–212, 214–216, Table V.).

There have been other cases of two succeeding parthenogenetic generations while the females were exposed to males in *P. texanus* and *A. eurycephalus* (not included in the attached data). It has been thought that a female might mutate in some way which would render her incapable of mating with a male of her own species. In such a case, she should reproduce by parthenogenesis. Then, if her progeny, due to the same mutation, could not mate back to the males of the original stock, and parthenogenesis should go on till the occasional male appears (see items 226, 226a, Table

V., and mating 5027, Nabours, 1925), the "event for which we wait" (Bateson, 1922) might be achieved. However, it is likely that the cases of succeeding generations by parthenogenesis, although the females were exposed to males, were due to impotency of the males rather than to mutations in the females. Nevertheless, there may be possibilities in this direction.

The hypothesis of Peacock and Harrison that parthenogenesis is consequent upon hybridity (loc. cit.) has probably received further support from the results of the parthenogenetic breeding of *P. texanus,* as described, if it be provided in addition *that the process of hybridism may bring together specific complementary, or climaxing genes which are responsible for, or cause the development of unfertilized eggs.*

Summary and Conclusions.

1. There is indication of a genetic factor, or a group of complementary factors responsible for parthenogenesis in these grouse locusts.

2. The hypothesis of Peacock and Harrison (1925, 1926) that parthenogenesis is consequent upon hybridity is probably further supported if it be provided, as these authors did not, that it is necessary to bring together in the processes of hybridism the specific complementary, or climaxing genetic factors which may cause the development of unfertilized eggs.

3. The members of the species *Paratettix texanus* Hancock are bisexual, the fertilized eggs producing males and females in equal numbers, and parthenogenetic, the unfertilized eggs, with rare exceptions, hatching females.

4. A mated female may have part of her ova fertilized, and also produce from unfertilized ova, by parthenogenesis, an additional number of offspring which are nearly always females.

5. The segregation and crossing over of factors occur in individuals reproducing by parthenogenesis to the same extent as in those reproducing bisexually.

6. If fertilized, the egg proceeds with the second polocyte division and develops bisexually. In the absence of the fertilizing sperm the last polyocyte division does not occur, or if it does the polar body is not eliminated. If the specific complementary gene,

or genes responsible for initiating parthenogenesis be present, diploidy is retained, or restored, and development may begin, consequentially as a kind of *artificial* parthenogenesis.

7. The progeny from unfertilized eggs are usually homozygous for all the factors they carry, though rarely one proves to be heterozygous for factors.

LITERATURE CITED.

Bateson, Wm.

'22 Evolutionary Faith and Modern Doubts. Science, 55: 55–61.

Bellamy, A. W.

'17 Multiple Allelomorphism and Inheritance of Color Patterns in *Tettigidea*. Jour. Genetics, Vol. VII., No. 1, pp. 55–70.

Cuénot, L.

'09 Les Males d'abeilles proviennent—ils toujours d'oeufs parthenogenetiques. Bull. Sci. France et Belg., XLIII.

Haldane, J. B. S.

'20 Note on a case of Linkage in *Paratettix*. Jour. Genetics, Vol. X., No. 1, pp. 47–51.

Hancock, J. L.

'02 The *Tettigidæ* of North America. Chicago, 188 pp.

Harman, Mary T.

'15 Spermatogenesis in *Paratettix*. Biol. Bull., Vol. XXIX., pp. 262–277.

Nabours, Robert K.

'14 Studies of Inheritance and Evolution in Orthoptera I. *Paratettix texanus*. Jour. Genetics, Vol. III., No. 3, pp. 141–170.

'17 Studies of Inheritance and Evolution in Orthoptera II. and III.: *Paratettix texanus* and a Mutant. Jour. Genetics, Vol. VII., No. 1, pp. 1–54.

'19 Parthenogenesis and Crossing Over in the Grouse Locust *Apotettix*. Am. Nat., Vol. LIII., No. 625, pp. 131–142.

'23 A New Dominant Color Pattern and Combinations that Breed True in the Grouse Locusts. Genetica, Vol. V., Nos. 5 and 6, pp. 477–480.

'25 Studies of Inheritance and Evolution in Orthoptera. V. The Grouse Locust, *Apotettix curycephalus* Hancock. Kan. Agri. Exp. Sta., Tech. Bull. 17: 1–231.

'27 Polyandry in the Grouse Locust, *Paratettix texanus* Hancock, with Notes on the Inheritance of Acquired Characters and Telegony. Am. Nat., Vol. LXI., pp. 531–538.

'29 The Genetics of the Tettigidæ (Grouse Locusts). Bibliographica Genetica, Vol. 5, pp. 27–101.

Nabours, Robert K., and Snyder, Bertha.

'28 Parthenogenesis and the Inheritance of Color Patterns in the Grouse Locust, *Telmatettix azteeus* Saussure. Genetics, Vol. XIII., pp. 126–132.

Newell, Wilmon.

'14 Inheritance in the Honey Bee. Science, N. S., Vol. XLI., No. 1049, pp. 218–219.

Peacock, A. D., and Harrison, J. W. Heslop.

'25 On Parthenogenesis Originating in Lepidopterous Crosses Trans. Nat. Hist. Soc. Northumberland, Durham and New Castle-upon-Tyne, N. S., 6, Part II.

'26 Hybridity, Parthenogenesis and Segregation. Nature, 117: 378–379.

Perez.

'79 The Theory of Dzierzon. Am. Bee Jour., XV.

Robertson, W. R. B.

'15 Chromosome Studies, III. Inequalities and Deficiencies in Homologous Chromosomes: Their Bearing upon Synapsis and the Loss of Unit Characters. Jour. Morph., Vol. XXVI., pp. 109–141.

'29 Chromosome Studies, V.: The Retention of Diploidy in Partheno-produced *Tettigidæ,* including two rare males, and the Tendency of Chromosomes to Persist in Their Original Gametic Position in the Cells of These and Their Biparentally Produced Relatives (*Apotettix eurycephalus* and *Paratettix texanus*). (In manuscript.)

Whiting, P. W.

'21*a* Studies on the Parasitic Wasp, *Hadrobracon brevicornis* (Wesmael), I. Genetics of an Orange-eyed Mutation and the Production of Mosaic Males from Fertilized Eggs. Biol. Bull., Vol. XLI., No. 1, pp. 42–54.

'21*b* Studies on the Parasitic Wasp, *Hadrobracon brevicornis* (Wesmael), II. A Lethal Factor Linked with Orange. Biol. Bull., Vol. XLI., No. 3, pp. 153–155.

Wilson, Edmund B.

'25 The Cell in Development and Heredity. Macmillan, New York, 1232 pages.